

# Why *Carcinus maenas* cannot get a grip on South Africa's wave-exposed coastline

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The European green crab *Carcinus maenas* has established considerable breeding populations in harbours and sheltered bays in the South-Western Cape, South Africa, but appears unable to flourish on the wave-exposed coastline. This study compares the abilities of *C. maenas* and those of an indigenous rocky-shore crab, *Plagusia chabrus*, to resist hydrodynamic forces. *C. maenas* had less than half the vertical tenacity of *P. chabrus* (371.5g and 780.5g respectively) and was unable to grip against as fast a unidirectional flow

(0.23m s<sup>-1</sup> vs 0.53m s<sup>-1</sup>) as *P. chabrus*. *C. maenas* also has significantly shorter and lighter limbs than *P. chabrus* and the dactyls of its walking legs are poorly adapted to grip onto rocky substrata. We conclude that *C. maenas* is poorly adapted to survive in wave-swept conditions and hence unlikely to displace indigenous crab species along the open wave-exposed coastline of South Africa. However, it may invade other sheltered locations, particularly Saldanha Bay and False Bay.

**Keywords:** *Carcinus maenas*, invasive species, tenacity, wave exposure

## Introduction

The European green crab *Carcinus maenas* is native to the eastern North Atlantic, North Sea and Baltic (Behrens Yamada 2001), but over the past two centuries has successfully invaded many coasts around the world, including the east and west coasts of North America (Cohen *et al.* 1995), Australia (Walton *et al.* 2002), and the south-west coast of South Africa (Le Roux *et al.* 1990). *C. maenas* is listed by both the Global Invasive Species Programme and the Global Ballast Water Management Programme as one of their 'ten most unwanted species'.

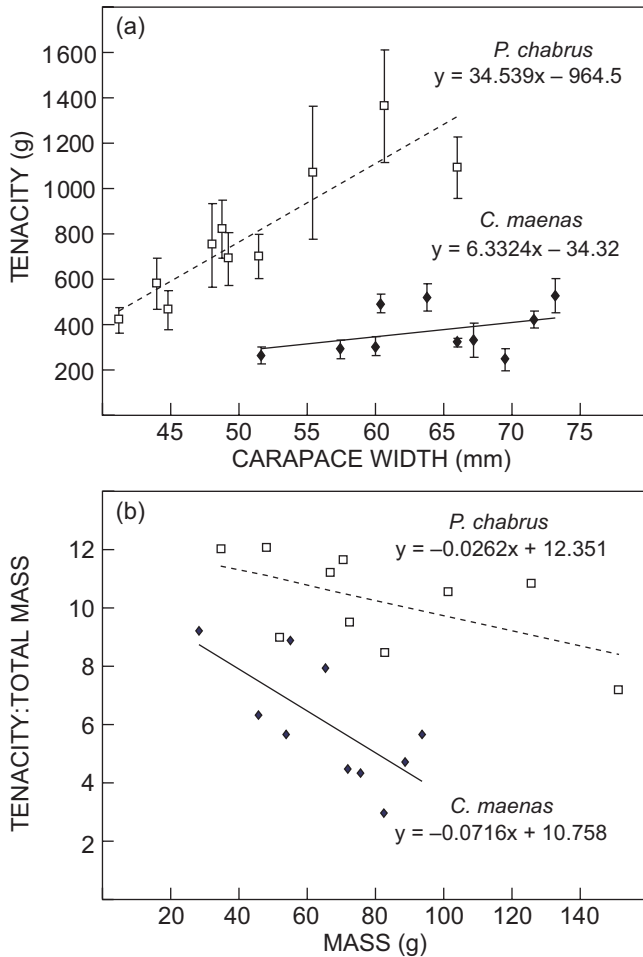
The South African invasion by *C. maenas* was first noticed in Table Bay Docks, Cape Town in 1983 (Joska and Branch 1986, Le Roux *et al.* 1990). A year later, breeding populations were recorded 15km north in Blouberg and since then they have been found in Camps Bay, Sea Point, Mouille Point, Green Point (all in Table Bay) and in Hout Bay Harbour, with vagrant individuals twice recorded in Saldanha Bay (Griffiths *et al.* 1992, Robinson *et al.* 2004). Thus, more than 20 years after its introduction, the distribution of *C. maenas* remains limited to sheltered bays, harbours or wave-protected areas close to the original site of introduction. It has largely failed to establish or compete with indigenous crabs along the generally very linear and wave-exposed South African coastline (Le Roux *et al.* 1990, Robinson *et al.* 2005). In its native range and in the other areas it has invaded, wave-exposure may also limit its distribution to sheltered or semi-exposed habitats (Crothers 1968, Griffiths *et al.* 1992, Grosholz *et al.* 2000).

If *C. maenas* is limited by wave-exposure, the obvious question is: why? Other species native to South Africa's coastline, such as *Plagusia chabrus*, the most abundant native crab found in sites colonised by *C. maenas*, do not seem to be limited by wave action and are found clinging to rock surfaces in extremely wave-swept locations (Griffiths *et al.* 1992).

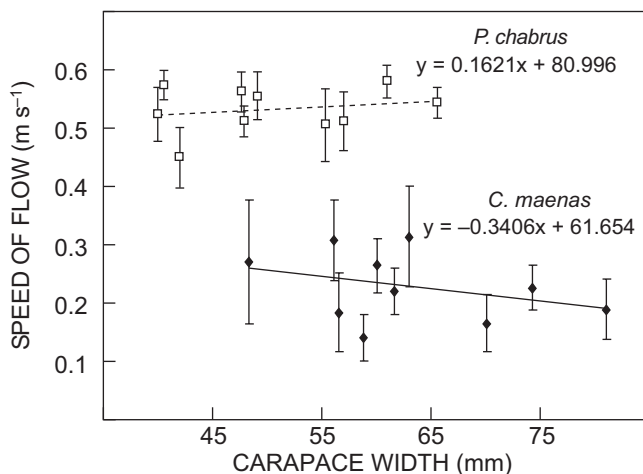
We compare the abilities of *C. maenas* and *P. chabrus* to actively grip a rock surface against a vertical force and to withstand unidirectional flow. The relative leg length (stance), leg mass (strength) and shape of the dactyls are also compared between the two species. On the basis of these results, we speculate on the potential for future spread of *C. maenas*.

## Material and Methods

*C. maenas* were collected from Table Bay Harbour using crab traps baited with sardine *Sardinops sagax*. *P. chabrus* were collected in the same way, or by divers, from Kalk Bay Harbour in False Bay. Only individuals with all limbs intact were included in the analysis. Crabs were returned to the University of Cape Town, where they were kept in a closed-circuit re-circulating aquarium at 12°C. If held for more than 12h, they were fed with sardine or mussels. Ten *C. maenas* and 10 *P. chabrus* were used in the tenacity experiments, and a different 10 crabs of each species in the flume experiments. Thirty-one crabs of each species were frozen overnight and used for morphological analysis.



**Figure 1:** (a) Vertical tenacity of *P. chabrus* and *C. maenas* in relation to carapace width; (b) relationship between tenacity per unit body mass and crab mass for *P. chabrus* and *C. maenas*. Error bars denote  $\pm$ SD

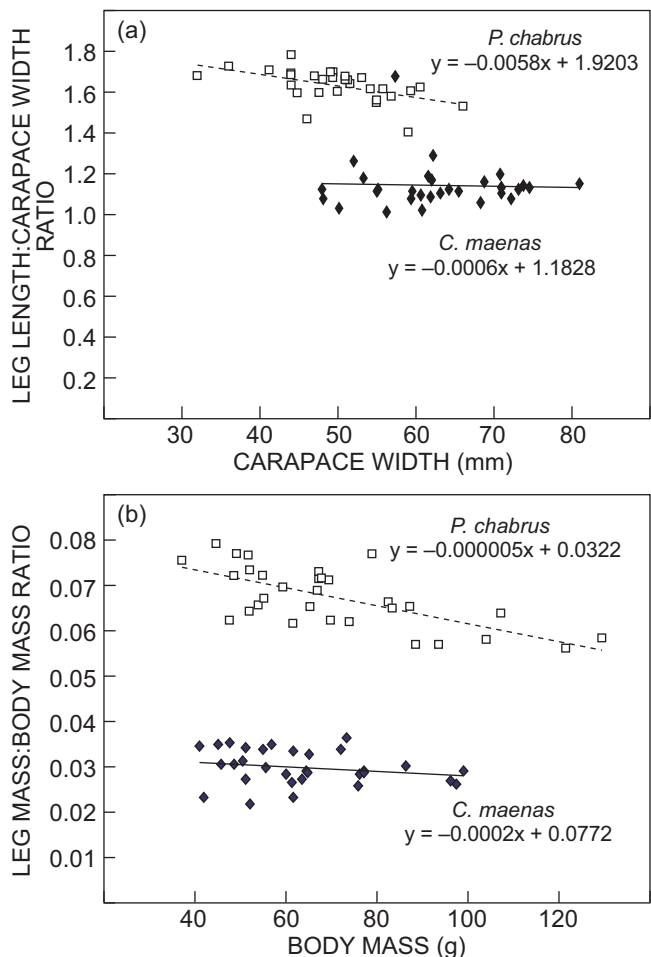


**Figure 2:** Unidirectional flow withstood before failure of grip in the crabs, *P. chabrus* and *C. maenas*, as related to carapace width. Error bars denote  $\pm$ SD

Vertical tenacity was measured by tying a loop of nylon line around the body of each crab. Crabs were then allowed approximately 30 seconds to settle on a large rough rock, submerged in seawater. They were then pulled vertically until they were dislodged. A spring balance, accurate to the nearest 50g and attached to the nylon line, measured the maximum force required to dislodge the crab. Five replicate readings were taken from each of 10 crabs of each species.

Horizontal tenacity was measured in a seawater flume around which water was pumped in one direction. Crabs were tethered to the top of the flume chamber using nylon line tied around their bodies between the second and third pairs of walking legs. The tether allowed the crabs movement, but restricted them to the central portion of the flume chamber. A single sheet of sandpaper was used to standardise the surface inside the chamber and was regularly replaced with another sheet of the same make and abrasiveness.

Each crab was allowed to settle in the flume for 30 seconds before the current was switched on. The current was then increased by 5% at successive five-minute inter-



**Figure 3:** (a) Relationships between leg-length to carapace-width ratio and carapace width in *P. chabrus* and *C. maenas*; (b) relationship between leg-mass to body-mass ratio and body mass in the crabs *P. chabrus* and *C. maenas*

vals. The crab's grip was recorded to have failed if at least six of the walking legs lost contact with the sandpaper.

Each of the eight walking legs of 31 crabs per species was straightened and measured from the base to the tip of the dactyl, using Vernier callipers. Carapace width (CW) was measured at the widest point. Average leg length was divided by carapace width to determine a leg-length to body-width ratio. The same crabs were used to determine a leg-mass to body-mass ratio. Each leg was separated from the crab and weighed individually on a scale ( $\pm 0.01\text{g}$ ) and average leg mass calculated. The body of the crab was weighed independently and leg-mass to body-mass ratios calculated. The dactyls of the walking legs were sketched with a camera-lucida.

## Results

The vertical forces needed to dislodge *P. chabrus* were consistently three times greater than for *C. maenas* of equivalent carapace width (Figure 1a). There was a strong positive relationship between tenacity and CW in *P. chabrus* — crabs of 60mm CW having a grip more than 2.5 times that of crabs of 40mm (1 107g and 417g respectively) ( $t = 5.59$ ,  $df = 8$ ,  $p = 0.00$ ). By contrast, there was no significant relationship between CW and vertical tenacity in *C. maenas*, and tenacity ranged between 200g and 400g ( $t = 1.21$ ,  $df = 8$ ,  $p = 0.26$ ). When vertical tenacity was expressed as a function of body mass (Figure 1b), *P. chabrus* again showed a much stronger grip per unit mass (mean tenacity 10.1 times body mass) than *C. maenas* (6.8 times). Expressed as a function of mass, tenacity decreased steeply with increasing size in *C. maenas* ( $t = -2.81$ ,  $df = 8$ ,  $p = 0.02$ ), but not for *P. chabrus* ( $t = -2.00$ ,  $df = 8$ ,  $p = 0.08$ ).

*P. chabrus* withstood nearly two times higher horizontal flow velocities than *C. maenas* (Figure 2), but there was no significant relationship between size and flow velocity in either species (*P. chabrus*:  $t = -1.03$ ,  $df = 8$ ,  $p = 0.33$ ; *C. maenas*:  $t = -0.65$ ,  $df = 8$ ,  $p = 0.53$ ).

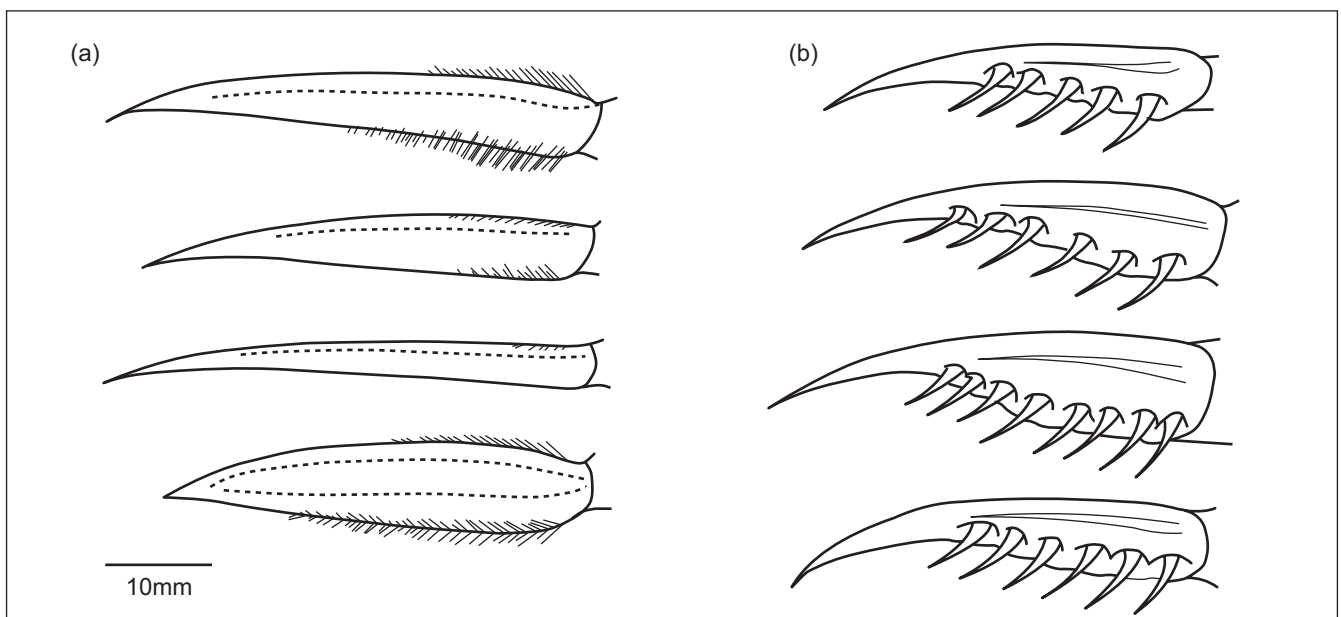
*P. chabrus* had significantly ( $t = 19.74$ ,  $df = 60$ ,  $p = 0.00$ ) longer legs than *C. maenas* (average values 1.631mm and 1.142mm respectively; Figure 3a). Relative leg length decreased significantly in larger *P. chabrus* ( $t = -3.48$ ,  $df = 29$ ,  $p = 0.00$ ), but not in *C. maenas* ( $t = -0.26$ ,  $df = 29$ ,  $p = 0.8$ ; Figure 3a).

Relative to body mass, *P. chabrus* legs were nearly twice as heavy as *C. maenas* legs ( $t = 27.34$ ,  $df = 60$ ,  $p = 0.00$ ) and relative leg-mass decreased in larger *P. chabrus* ( $t = -4.96$ ,  $df = 29$ ,  $p = 0.00$ ), but not in *C. maenas* ( $t = 1.20$ ,  $df = 5$ ,  $p = 0.24$ ; Figure 3b). *P. chabrus* had thick spines and sharp curved dactyls compared to blunter less spinose dactyls in *C. maenas* (Figure 4).

## Discussion

Crabs in a wave-swept environment are constantly in danger of being overturned or swept away as a result of hydrodynamic forces (Martinez *et al.* 1998, Dickinson *et al.* 2000, Lau and Martinez 2003). *P. chabrus* is found on exposed and sheltered shores, whereas *C. maenas* is conspicuously absent from exposed shores. Our aims were to test if *C. maenas* is physically less able to deal with hydrodynamic forces than *P. chabrus* and, hence, to explain why its distribution is limited to sheltered bays, harbours and lagoons in the South-Western Cape.

The vertical force required to dislodge *C. maenas* was indeed less than half that required for *P. chabrus* of the same carapace width. Active grasping, especially on rugose



**Figure 4:** Dactyls of periopods 1–4 of (a) *C. maenas* and (b) *P. chabrus* of carapace widths of 61.2mm and 55.0mm respectively

rocks, is an important behavioural adaptation to life in wave-swept environments (Martinez 2001), so this may well explain why *C. maenas* are unable to tolerate the wave forces experienced by *P. chabrus* on exposed rocky coasts. The negative tenacity to body mass relationship in *C. maenas* (but not in *P. chabrus*) further suggests that larger *C. maenas* will have even more difficulty in gripping onto rocks when hydrodynamic forces increase compared to smaller individuals and *P. chabrus*.

Our second experiment tested the ability of crabs to withstand unidirectional flow, which generates forces of both drag and lift. *P. chabrus* was clearly able to better withstand unidirectional flows than *C. maenas*, but the absolute values need to be treated with caution. In nature, crabs have to deal with the added complications of acceleration reaction of the water resulting from wave action (Lau and Martinez 2003) and also need to contend with a wide range of substrata. Moreover, they have to remain mobile in order to mate, feed and escape predation. The flume experiment used only a unidirectional flow and a standardised artificial substratum. Whereas ideal for comparative purposes, these do not represent natural conditions. It is also worth noting that the angle at which crabs face a current may influence the velocity they can withstand (Lau and Martinez 2003). Live crabs were used in our experiments (unlike the work done on *Grapsus tenuicrustatus* and *Pachygrapsus crassipes* by Martinez 2001, Lau and Martinez 2003), and thus assumed that the crabs would naturally optimise their stance to avoid losing contact with the surface (Dickinson *et al.* 2000, Martinez 2001, Lau and Martinez 2003).

The leg-length to body-width ratio gives an indication of the maximum lateral stance available to an animal. Longer legs allow for a more lateral stance to increase manoeuvrability (Dickinson *et al.* 2000) and stability (Martinez *et al.* 1998, Martinez 2001). Martinez (2001) showed that *G. tenuicrustatus* changed its posture depending on whether it was moving through water or on land. In water, it widened its stance, increasing its stability and therefore decreasing the possibility of being overturned or washed away. This posture also decreased the drag experienced while underwater (Martinez 2001). *P. chabrus* has considerably longer legs than *C. maenas* (Figure 3a), implying that it can adopt wider postures to enhance tenacity (Figures 1, 2). It also has heavier legs than *C. maenas*, indicating greater muscle volume and hence grip. Thus, both stance and strength will favour *P. chabrus* when hydrodynamic forces increase.

The curved ends and thick spines on the dactyls of *P. chabrus* also appear better adapted to grip the substratum than the blunter less spinose dactyls of *C. maenas*, and the sharp tips may aid grip in small holes and crevices. The dactyls of the last pair of legs in *C. maenas* are flattened, a characteristic typical of the Portunidae (swimming crabs), where the last pair of legs is usually held horizontally, and is rarely used for walking. By contrast, *P. chabrus*, a grapsid (shore) crab, has similar dactyls on all walking legs and uses all four pairs to grip the substratum.

Our study suggests that *C. maenas* is less able than *P. chabrus* to resist both vertical and horizontal hydrodynamic

forces, and that the root of these differences lie in its morphology. We suggest that *C. maenas* is therefore likely to remain confined to protected harbours and bays along the South African coast. *P. chabrus* is able to inhabit areas that are unsuitable to *C. maenas*, suggesting that the indigenous species will not be competitively excluded from the open coast (as it appears to have been in Table Bay Docks — unpublished data from Robinson *et al.* 2005).

**Acknowledgements** — Thanks to T Robinson for invaluable help in all aspects of this work and to the National Research Foundation, the Department of Science and Technology, and the Centre of Excellence for Invasion Biology, University of Cape Town, for financial support.

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